Construction of a *Saccharum* Consensus Genetic Map from Two Interspecific Crosses

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ABSTRACT

A consensus map of homologous DNA linkage groups from two genotypes in each of two *Saccharum* species was aligned with the compact diploid genome of *Sorghum bicolor* (L.) Moench. A set of 439 DNA probes from different Poaceae (grasses) detected 2523 loci in two segregating populations derived from the crosses *Saccharum officinarum* L.'Green German' × *S. spontaneum* L. 'IND 81-146', and *S. spontaneum* 'PIN 84-1' × *S. officinarum* 'Muntok Java'. Genetic maps of the four *Saccharum* genotypes, including a total of 289 linkage groups (LGs), were assembled into 13 *homologous groups* (HGs) on the basis of parallel arrangements of duplicated loci. The consensus map of HGs consisted of 232 probes and 982 mapped loci/alleles in four sugarcane linkage maps. Of the 982 loci/alleles on the consensus map, 845 (86%) of them correspond to a single linkage group of *Sorghum*, indicating the highly conserved genome structure between these two closely related genera. At least six basic chromosomes, LGs A, D, F, H, I, and J, showed close correspondence to each other in *Saccharum* and *Sorghum*. Two possible chromosome fusion events were found in *S. spontaneum* corresponding to sorghum LG B fused with LG E, and LG B fused with LG G. This consensus map illustrates how the high-density sorghum linkage map can be used to facilitate the mapping and understanding of the complex sugarcane genome.

The number of species recognized in the genus *Saccharum* depends on the criteria used for classification. Six old world species of *Saccharum* are often recognized (Roach and Daniels, 1987). Two wild *Saccharum* species *S. spontaneum* (2*n* = 36–128) and *S. robustum* Brandes & Jesw. ex Grassl (2*n* = 60–170) probably originated from India and New Guinea, respectively (Sreenivasan et al., 1987; Roach, 1995). The cultivated species *S. officinarum* (2*n* = 70–140) is thought to be derived from *S. robustum* (Irvine, 1999). The remaining two cultivated species, *S. barberi* Jesw. and *S. sinense* Roxb., are believed to be natural hybrids of *S. spontaneum* and *S. officinarum* (Sreenivasan et al., 1987; Roach, 1995; Irvine, 1999). The species *S. edule* Hassk. (2*n* = 60, 70, 80, and some aneuploids), noted for its aborted inflorescence, may be a hybrid of *S. officinarum* or *S. robustum* with *Miscanthus* sp. (Daniels and Roach, 1987). More detailed taxonomic and molecular analyses led to the suggestion of condensing the six *Saccharum* species into two (Irvine, 1999). One species consists only of *S. spontaneum* on the basis of chloroplastic (Sobral et al., 1994), mitochondrial (D'Hont et al., 1993), and ribosomal DNA (Glaszmann et al., 1990). The other is considered as *S. officinarum*, including *S. officinarum*, *S. robustum*, and the other three species that are all postulated to be interspecific hybrids.

Recently, evidence generated from quantitative karyotyping (Ha et al., 1999) and fluorescence in situ hybridization (D'Hont et al., 1995a,b, 1998; Ha et al., 1999) suggests that the basic chromosome number (*x*) for *Saccharum* is *x* = 8 for *S. spontaneum* and *x* = 10 for *S. officinarum* and *S. robustum*. These two sets of basic chromosome numbers correspond to the chromosome numbers in these two horticultural classes. Of the 1086 *S. spontaneum* samples for which chromosome counts were available, 77% are multiples of eight (2*n* = 40, 48, 56, 64, 72, 80, 88, 96, 112, 120, and 128). Of the 96 *S. robustum* samples, 72% are multiples of 10 (2*n* = 60, 70, 80, 90, 100, 110, 140, and 170), and 92% of the 497 *S. officinarum* samples are also multiples of 10 (2*n* = 80) (Irvine, 1999). In the Andropogoneae tribe, *x* = 10 is common (Whalen, 1991) but exceptions exist, such as 2*n* = 6 and 8 for *Iseilema* (Clayton and Renvoize, 1986).

Linkage mapping in sugarcane has been carried out on five populations generating seven linkage maps by means of mostly single dose restriction fragment (SDRF) markers (Wu et al., 1992). The first sugarcane linkage map was constructed from the progeny of a cross between *S. spontaneum* 'SES208' (2*n* = 64) and its doubled haploid ADP068 (Da Silva et al., 1993; Al-Janabi et al., 1993). This map consists of 64 linkage groups assembled into eight homologous groups (HGs) based on 276 restriction fragment length polymorphisms (RFLP) and 208 single dose (SD) arbitrarily primed polymerase chain reaction (PCR) loci (Da Silva et al., 1995). The second map was derived from the progeny of a self-pollinated cultivar 'R570' (2*n* = 107–115). This map consists of 408 RFLP loci on 96 linkage groups and 10 putative homologous groups (Grivet et al., 1996). A third map of *S. officinarum* 'Louisiana Purple' (2*n* = 80) based on a cross with *S. robustum* consists of 160 random amplified polymorphic DNA (RAPD) markers and one morphological marker assembled in 51 linkage groups (Mudge et al., 1996). Four additional maps were constructed for each of the four parents from two inter-

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Abbreviations: cM, centiMorgan; G×I, 'Green German' × 'IND 81–146'; GG, 'Green German'; HG, homologous groups; IND, 'IND 81–146'; LG, linkage group; MJ, 'Muntok Java'; P×M, 'PIN 84–1' × 'Muntok Java'; PCR, polymerase chain reaction; PIN, 'PIN 84–1'; QTL, quantitative trait loci; RAPD, random amplified polymorphic DNA; RFLP, restriction fragment length polymorphism; SD, single dose.

specific crosses *S. officinarum* 'Green German' (GG, $2n = 97–117$) × *S. spontaneum* 'IND 81–146' (IND, $2n = 52–56$) and *S. spontaneum* 'PIN 84–1' (PIN, $2n = 96$) × *S. officinarum* 'Muntok Java' (MJ, $2n = 140$). A total of 72, 69, 72, and 69 linkage groups were assembled from 615, 536, 575, and 418 RFLP markers for GG, IND, MJ, and PIN, respectively (Ming et al., 1998).

Among these seven sugarcane linkage maps, the number of linkage groups in the first two maps is expected to be the same as the number of 2*n* chromosomes. Because the first map is based on progeny derived from a cross between a doubled haploid and its mother plant, and the second map is based on the progeny of a self-pollinated elite cultivar, the full set of 2*n* chromosomes was transmitted to their progeny. The number of linkage groups in the other five maps, however, is expected to be half of the parental 2*n* chromosome number, since only half the chromosomes were transmitted to the segregating F_1 populations used in mapping. A comparative analysis between the sorghum linkage map and the five sugarcane linkage maps indicates that every one of the sugarcane maps is incomplete (Ming et al., 1998).

Although the basic chromosome number(s) of *Saccharum* are known, complete genetic maps reflecting these basic chromosome numbers are still not available. As an approach towards developing more complete sugarcane maps, we earlier constructed four sugarcane maps using the same set of DNA probes that were mostly mapped in sorghum. Each of these four maps covered only 39.5 to 46% of the *Saccharum* genome, but collectively they covered 70% of the genome (Ming et al., 1998). A consensus genetic map of Saccharum will provide a working map with the highest genome coverage to date and a set of anchor markers for future genetic and QTL mapping. We report here using the sorghum linkage groups as a template to construct a consensus genetic map of sugarcane assembled from our earlier four linkage maps of the two species from which the modern sugarcane varieties derived.

MATERIALS AND METHODS

Plant Materials

Two interspecific mapping populations each derived from crosses between heterozygous parents were used. Genomic DNA was analyzed from (i) 85 segregating plants from *S. officinarum* 'Green German' (GG, $2n = 97–117$) × *S. spontaneum* 'IND 81–146' (IND, $2n = 52–56$) and (ii) 85 segregating plants from *S. spontaneum* 'PIN 84–1' (PIN, $2n = 96$) × *S. officinarum* 'Muntok Java' (MJ, $2n = 140$). These two populations 'Green German' × 'IND 81-146' (G×I) and 'PIN 84-1' × Muntok Java' (P×M) were grown at Weslaco, Texas from November 1994 to February 1996. The classification of GG and MJ as *S. officinarum* is based on Irvine's definition (1999).

Genotyping

A total of 844 DNA probes were surveyed on G×I and P×M, including cDNA and genomic clones from sugarcane, sorghum, maize (*Zea mays* L.), rice (*Oryza sativa* L.), barley (*Hordeum vulgare* L.), and oat (*Avena sativa* L.). Probe-enzyme combinations which generated the largest numbers of polymorphic bands were chosen for mapping. A total of 440 probes were mapped in two interspecific sugarcane populations. Twelve new DNA probes were added to previously described sugarcane maps (Ming et al., 1998).

Data Analysis

Methods for linkage mapping and data analysis were previously described (Ming et al., 1998). The nomenclature of HGs 1 to 17 was consistent with the previously published sugarcane genetic maps. HG 18 was newly formed after mapping more markers on sugarcane maps.

Assembly of Homologous Groups

Homologous groups were first assembled within each parental variety. Any two or more linkage groups that share at least two common markers detected by two different probes were assigned to the same homologous group. Once a preliminary homologous group was established, any linkage group sharing two markers on the homologous group, either from the same or different linkage groups, was added to this homologous group.

Since eight of the 10 primary homologous groups were shared by *S. officinarum* and *S. spontaneum* (Ming et al., 1998), the homologous groups across parental varieties and species were established on the basis of two or more common markers. The unassigned linkage groups were checked against these ''unified'' homologous groups and added to the homologous group if they shared at least two common markers.

Assembly of Consensus Map

The longest linkage group or groups of a HG were used as a backbone to assemble our consensus genetic map of sugarcane. Other linkage groups were added to the consensus map on the basis of the relative position of the common markers used to form the HG. Markers detected by the same probe were considered as single locus if their relative positions were within 5 cM (centiMorgans) in two or more LGs, or as *repeated* loci if their positions were beyond 5 cM relative to other linked markers. Because the consensus map positions of these markers were based on their relative positions on different linkage groups, they may or may not be truly duplicated. Therefore, this type of markers is designated tentatively as *repeated* markers. Only the markers detected by a probe that mapped on the same chromosome were referred as duplicated markers.

RESULTS

Linkage Mapping

Since constructing our initial sorghum and sugarcane comparative maps (Ming et al., 1998), we have mapped 12 more probes to produce an additional 18, 10, 20, and 14 loci mapped in GG, MJ, IND and PIN, respectively. From the total of 440 probes mapped in two mapping populations, 321 probes generated 634, 582, 555, and 431 RFLP markers. The remaining 119 probes failed to produce polymorphic or readable fragments despite survey filters showing polymorphism between parental varieties. The total number of linkage groups mapped were 75, 73, 69, and 72 with total length in Kosambi centiMorgans of 2466, 1472, 2172, and 1395 for GG, MJ, IND, and PIN, respectively (Table 1). The total of 289 linkage groups of these four linkage maps can be found

Table 1. Summary of sugarcane genome mapping data.

Species	*S. officinarum*		*S. spontaneum*		
Parental varieties	Green German	Muntok Java	IND 81-146	PIN 84-1	Total
Chromosome number (2*n*)	97-117	140	52-56	96	
Total DNA probes surveyed					844
Total DNA probes mapped					440
SDRF markers	434	359	395	308	
DDRF markers	132	159	54	86	
TDRF markers	19	24	3	9	
Other markers	49	40	103	28	
Total RFLP markers	634	582	555	431	
Total loci detected†	755	749	512	506	2523
Linkage groups based on SDRF markers	75	73	70	71	
SDRF markers linked to map	289	214	257	194	
Total length of all linkage groups (cM)	2466	1472	2172	1395	

† Excluding "other" markers for which segregation did not fit SD, DD, or TD ratios.

at http://www.plantgenome.agtec.uga.edu/sugarcane_maps.html (verified October 2, 2001).

Homologous Groups

Ten HGs consisting of 62 LGs were assembled for GG, eight HGs consisting of 49 LGs for MJ, nine HGs consisting of 48 LGs for IND, and 10 HGs consisting of 51 LGs for PIN were assembled for the *Saccharum* consensus map. Homologous groups 1, 2, 3, 4, 5, 9, and 15 were present in all four linkage maps. HG6 was present in GG, MJ, and IND. HG7 was present in GG and PIN. HG10 was present in GG, IND, and PIN. HG11 was present in GG and PIN. HG17 was present in PIN only. HG 18 was present in GG only (see http://www.plantgenome.agtec.uga.edu/sugarcane_maps.html).

The assembly of the homologous groups was accomplished with the sorghum linkage groups as templates as follows.

Table 2. Homologous loci shared among *Saccharum* HGs on four linkage maps and *Sorghum* LGs.

Sorghum	*Saccharum*		Number of shared loci				Total
LG	HG		MJ	IND	PIN	Sorghum	loci
A	GG	2	9	17	7	19	28
	MJ	2		11	10	14	21
	IND	2			12	22	36
	PIN	2				9	15
B	GG	4	6	7	5	7	13
	MJ	4		6	6	5	8
	IND	4			5	5	9
	PIN	4				7	11
	GG	11			2	3	9
	PIN	11				2	3
C	GG	3	21	25	18	34	52
	MJ	3		13	11	17	30
	IND	3			13	23	32
	PIN	3				14	24
D	GG	5	7	7	9	16	23
	MJ	5		6	8	9	13
	IND	5			5	14	19
	PIN	5				12	20
E	GG	18				3	6
	MJ	4				2	6
F	MJ	19				5	6
	IND	6				5	8
G	GG	1	7	4	6	8	14
	MJ	1		4	4	6	11
	IND	1			4	4	10
	PIN	1				7	9
	IND	15				2	5
H	GG	9	3	3	2	3	4
	MJ	9		4	1	6	9
	IND	9			3	5	13
	PIN	9				2	4
I	GG	7			2	4	6
	PIN	7				2	2
	PIN	17		3	1	3	7
J	GG	10		3	1	3	7
	IND	10			4	5	7
	PIN	10				6	6
Sum						313	502

Sorghum LG A and *Saccharum* HG 2

Three HGs were formed in GG on the basis of the presence of two or more common markers among linkage groups. These three HGs consisting of LGs 17 and 68, LGs 39 and 46, and LGs 10, 11, and 38, respectively, correspond to three parts of the sorghum LG A. Two HGs in MJ, one consisting of LGs 5 and 42 and the other consisting of LGs 12, 13, 32, and 37, correspond to two parts of sorghum LG A. One HG designated as HG 2 in IND correspond to 80% of the sorghum LG A. HG 2 consists of nine LGs, 4, 5, 18, 32, 35, 36, 37, 38, and 42. One HG in PIN consists of LGs 69, 71, and 72; another HG in PIN consists of LGs 46 and 50. These two HGs correspond to two parts of sorghum LG A.

Markers pSB1652 and pSB581 on IND LG 4 and GG LG 68 were used to link one of the two GG HGs to IND HG 2. Markers CDSR128 and CSU469 on IND LG 35 and GG LG 11 were used to link the other GG HG to IND HG 2. To date, a total of 17 common markers are shared between GG HG 2 and IND HG 2.

Markers CDSB3 and BNL9.11 on MJ LG 5 and IND LG 5 were used to link one of the two MJ HGs to IND HG 2. Markers CDSR128 and pSB79 on MJ LG 32 and IND LG 35 were used to link the other MJ HG to IND HG 2. A total of 11 common markers are shared between MJ HG 2 and IND HG 2.

Markers Sh2 and CDSR87 on PIN LG 49 and IND LGs 35 and 36 were used to link one of the two PIN HGs to IND HG 2. Markers pSB79 and pSB243 on PIN LG 46 and IND LG 35 were used to link the other PIN HG to IND HG 2. A total of 12 common markers are shared between IND HG 2 and PIN HG 2.

After a unified HG 2 was established across four linkage maps, 10 additional linkage groups were added on the basis of sharing two or more common markers

Table 3. Correspondence of homologous loci between sugarcane HGs and sorghum LGs.

HG	Parents	# of Probes	# of Loci scored	Mapped	# lgs mapped	# loci corresponding to sorghum LG									
						A	B	C	D	E	F	G	H	I	J
1	GG, MJ, IND, PIN	17	171	82	19	4	1	2	1	7	1	66	0	0	0
2	GG, MJ, IND, PIN	53	488	207	39	178	0	4	10	2	2	4	1	0	6
3	GG, MJ, IND, PIN	65	553	297	52	10	8	255	7	1	8	3	0	3	2
4	GG, MJ, IND, PIN	17	169	75	20	0	56	1	2	11	0	0	1	0	3
5	GG, MJ, IND, PIN	26	254	125	33	1	0	5	113	1	1	1	3	0	0
6	GG, MJ, IND	13	90	33	9	0	0	2	0	0	30	0	0	1	0
7	GG, PIN	4	42	16	4	0	0	1	0	0	0	0	0	15	0
9	GG, MJ, IND, PIN	11	105	59	13	3	1	0	1	1	1	0	49	0	2
10	GG, IND, PIN	10	80	41	9	0	1	1	0	0	0	0	3	0	36
11	GG, PIN	5	34	13	2	0	11	2	0	0	0	0	0	0	0
15	GG, MJ, IND, PIN	5	45	17	5	1	0	1	0	1	0	14	0	0	0
17	PIN	4	28	8	2	0	0	0	0	0	0	0	0	8	0
18	GG	2	22	9	2	1	0	0	1	5	0	2	0	0	0

between each individual LG and the unified HG 2. These 10 additional linkage groups are LGs 15 and 54 in GG; LG 4, 10, and 54 in MJ; LG 17 in IND and LGs 15, 30, 35, and 36 in PIN.

GG and MJ shared nine common markers on HG 2; GG and IND shared 17 markers, and GG and PIN shared seven markers. MJ and IND shared 11 common markers; and MJ and PIN shared 10 markers. IND and PIN shared 12 common markers (Table 2).

Nineteen of the 28 (68%) unique markers of GG HG 2 correspond to sorghum LG A; one unique marker (3.6%) corresponds to sorghum LG J; the other eight markers did not map in sorghum. Fourteen of the 21 (67%) markers on MJ HG 2 correspond to sorghum LG A; one marker (7.7%) each corresponds to sorghum LGs C, E, and J. Twenty-two of the 36 (61%) markers on IND HG 2 correspond to sorghum LG A; two (5.6%) correspond to sorghum LG G. Nine of the 15 (60%) markers on PIN HG 2 correspond to sorghum LG A; one (6.7%) corresponds to sorghum LG G.

A total of 53 probes on HG 2 detected 488 loci, and 207 (42%) of them were mapped on 19 LGs forming HG 2. Among the 207 loci mapped, 178 (86%) correspond to sorghum LG A (Table 3).

Sorghum LG B and *Saccharum* HGs 4 and 11

One HG in GG, consisting of LGs 41 and 47 corresponds to part of sorghum LG B, and is designated as HG 11. No original HG was formed in MJ. Two small HGs found in IND correspond to the same genomic region of sorghum LG B; one consists of LGs 29 and 34 and is designated as HG 4. The other HG consists of LGs 40 and 53. Two HGs in PIN, one consisting of LGs 29, 34, and 47, and the other consisting of LGs 25 and 26, correspond to two parts of sorghum LG B.

Markers CDSC49 and CDSR74 on IND LG 29 and PIN LGs 29 and 34 were used to link one of the two PIN HGs to IND HG 4. After forming this unified HG 4, markers CDSB7 and CDSR78 on HG 4 (IND LG 29 and PIN LG 34) and PIN LG 25 were used to link the second PIN HG to HG 4. Three LGs each from GG (LGs 28, 52, and 55) and MJ (LGs 31, 48, 53) shared two or more markers with HG 4 and thus added to the unified HG 4. Markers CSU13 and CBSR78 on HG 4 (GG LG 55 and PIN LG 34) and IND LG 53 linked the second IND HG to HG 4. With the expanded HG 4 as a template, three more LGs, GG LGs 27 and 56 and PIN LG 22, were added to HG 4.

PIN LG31 shared two markers, pSB101 and pSB103, with GG HG11. Only one marker, pSB103, was common between HGs 4 and 11, so these two HGs remain as independent groups.

GG and MJ shared six common markers on HG 4; GG and IND shared seven markers; and GG and PIN shared five markers. MJ and IND shared six common markers; and MJ and PIN shared six markers. IND and PIN shared five common markers.

Among the 13 unique markers of GG HG 4, seven (54%) correspond to sorghum LG B, while one (8%) corresponds to sorghum LG C. The remaining five markers did not map in sorghum. Five of the eight (63%) markers on MJ HG 4 correspond to sorghum LG B, while one (12.5%) corresponds to sorghum LG C and two (25%) correspond to sorghum LG G. Five of the nine (61%) markers on IND HG 4 correspond to sorghum LG B, while one (11%) corresponds to sorghum LG A. Seven of the 11 (64%) markers on PIN HG 4 correspond to sorghum LG B, while one each (9%) correspond to sorghum LGs A, C, and E.

A total of 17 probes on HG 4 detected 169 loci. Seventy-five (44%) of them were mapped on 20 LGs forming HG 4. Among the 75 loci mapped, 56 (75%) correspond to sorghum LG B, and 11 (15%) correspond to sorghum LG E.

A total of 5 probes detected 34 loci on HG 11. Thirteen (38%) of them were mapped on 2 LGs forming HG 11. Among the 13 loci mapped, 11 (85%) correspond to sorghum LG B.

Sorghum LG C and *Saccharum* HG 3

Two HGs in GG, previously designated HGs 3 and 8 (Ming et al., 1998), correspond to two segments of sorghum LG C. GG HG 3 consists of seven LGs: 48, 49, 60, 61, 62, 63, and 69. GG HG 8 consists of 11 LGs: 1, 2, 3, 4, 7, 8, 9, 24, 25, 26, and 35. Two MJ HGs correspond to two parts of sorghum LG C. One HG consists of LGs 68, 69, 70, and 71 and the other consists of LGs 1, 2, 3, 6, 11, 25, and 49. Two HGs in IND correspond to two parts of sorghum LG C. One consists of LGs 43, 46, and 68 and the other consists of LGs 1,

2, 3, 27, 28, and 54. No HG in PIN corresponds to sorghum LG C.

Markers CDSB28 and CSU450 on GG LG 3, MJ LG 11, and IND LG 28 linked the previously named HGs 3 and 8 to a single unified HG 3. Markers SHO68 and RZ421 on MJ LG 3 and IND LG 68 linked the second HG in IND to HG 3. Markers SHO59 and SHO87 on MJ LG 68 and IND LG 68 then connect the second HG in MJ to HG 3. Additional eight LGs were linked to the unified HG 3, including GG LGs 43 and 70, and PIN LGs 1, 3, 16, 17, 44, and 69.

Seven additional LGs joined HG 3 including MJ LGs 55, 58, and 67, IND LGs 20 and 22, and PIN LGs 58 and 64. Markers CSU33 and SG305 linked MJ LG 55 and IND LG 20 to HG 3. Two common markers of former HG 8, CDSB4 and pSB239 on GG LG 70 and PIN LG 17, and former HG 3 on MJ LG 55 and IND LG 20 connected these two HGs to form a single unified HG corresponding to the full length of the sorghum LG C. The unified single HG is designated as HG 3.

The common markers on HG 3 were 21 shared between GG and MJ, 25 shared between GG and IND, and 18 shared between GG and PIN. Thirteen markers were shared between MJ and IND, and 11 between MJ and PIN. Thirteen markers were shared between IND and PIN.

GG and MJ shared 21 common markers on HG 3; GG and IND shared 25 markers; and GG and PIN shared 18 markers. MJ and IND shared 13 common markers; and MJ and PIN shared 11 markers. IND and PIN shared 13 common markers (Table 2).

Thirty-four (65%) of the 52 unique markers of GG HG 3 correspond to sorghum LG C, while two (3.8%) of the 52 markers correspond to sorghum LG A, and one each (1.9%) corresponds to sorghum LGs D and F. The remaining 14 markers did not map in sorghum. Seventeen (57%) of the 30 markers on MJ HG 3 correspond to sorghum LG C, while two (6.6%) of the 30 markers correspond to sorghum LG D. Twenty-three (72%) of the 32 markers on IND HG 3 correspond to sorghum LG C. Fourteen (58%) of the 24 markers on PIN HG 3 correspond to sorghum LG C, while one (4.1%) of the 24 corresponds to sorghum LG D (Table 2).

A total of 65 probes on HG 3 detected 553 loci, and 297 (54%) of them were mapped on 52 LGs forming HG 3. Among the 297 loci mapped, 255 (86%) correspond to sorghum LG C (Table 3).

Sorghum LG D and *Saccharum* HG 5

One HG in GG, previously designated HG 5, corresponds to a large portion of sorghum LG D. GG HG 5 consists of five LGs: 12, 50, 59, 66, and 67. Two HGs in MJ correspond to two parts of sorghum LG D. One consists of LGs 43 and 44 and the other consists of LGs 45, 46, and 59. One HG in IND, consisting of LGs 41, 51, 52, and 60, corresponds to part of sorghum LG D. One HG in PIN, consisting of LGs 6, 39, 40, 53, and 54, corresponds to part of sorghum LG D.

Markers UMC44 and CSU393 on GG LG 12 and PIN LG 40 linked GG and PIN HGs to one unified HG 5. Markers UMC44 and pSB1895 on PIN LG 40 and IND LGs 41 and 52 were used to add IND HG to the unified HG 5. Markers UMC44 and pSB121 PIN LGs 40 and 53 and MJ LG43 were used to add one of the MJ HGs to HG 5, while markers RZ17 and pSB1895 on GG LG 59, PIN LG 40, and MJ LG 46 linked the second MJ HG to HG 5. Using the unified HG 5 as a template, we found an additional 12 LGs could be added to HG 5, including GG LGs 6, 40, and 58; MJ LGs 34 and 51; IND LGs 15 and 49; and PIN LGs 45, 51, 52, 65, and 66.

GG and MJ shared seven common markers on HG 5; GG and IND shared seven markers; and GG and PIN shared nine markers. MJ and IND shared six common markers; and MJ and PIN shared eight markers. IND and PIN shared five common markers.

Among the 23 number markers of GG HG 5, 16 (70%) correspond to sorghum LG D, while one each (4.3%) corresponds to sorghum LGs C and J. The remaining five markers did not map in sorghum. Nine (69%) of the 13 unique markers on MJ HG 5 correspond to sorghum LG D, while one (7.7%) corresponds to sorghum LG C. Fourteen (74%) of the 19 markers on IND HG 5 correspond to sorghum LG D, and none of these corresponds to another sorghum LG. Twelve (60%) of the 20 markers on PIN HG 5 correspond to sorghum LG D, while one (5%) corresponds to sorghum LG E.

A total of 26 probes on HG 5 detected 254 loci, and 125 (49%) of them were mapped on 33 LGs forming HG 3. Among the 125 loci mapped, 113 (90%) correspond to sorghum LG D.

Sorghum LG E and *Saccharum* HGs 4 and 18

Two HGs in GG, one previously designated HG 4 and the other newly designated as HG 18, correspond to parts of sorghum LG E. GG HG 4 was mostly corresponding to sorghum LG B, and only two loci detected by the same probe CDSR91 correspond to sorghum LG E. Part of the MJ HG 4 corresponds sorghum LG E consisting of LGs 28 and 34. No HG in IND or PIN was formed that corresponds to sorghum LG E.

GG HG 18 consists of two LGs: 73 and 76. Two (50%) of the four unique markers on MJ HG 18 correspond to sorghum LG E, while the other two (50%) correspond to sorghum LG G.

Two probes on HG 18, MZY14-1 and CSU539, detected 22 loci, and nine (41%) of them were mapped on seven LGs. Five (56%) of the nine loci correspond to sorghum LG E, and two (22%) correspond to sorghum LG E. The third probe on HG 18, CDSB31, detected 15 loci, and seven of them were mapped on six LGs. Six (86%) of the seven loci correspond to sorghum LG G, and the remaining one locus correspond to sorghum LG E. The fourth probe on HG 18, SG155, detected 18 loci, and nine (50%) of them were mapped on nine LGs. Seven (78%) of the nine loci correspond to sorghum LG G, While one each corresponds to sorghum LGs C and E.

Sorghum LG F and *Saccharum* HGs 6

One HG in MJ, previously designed as HG 6, consists of LGs 22 and 23. This HG corresponds to parts of

sorghum LG F. One HG in IND, consisting of LGs 10, 11, 66, and 70, corresponds to sorghum LG F. No original HG in GG or PIN corresponds to sorghum LG F.

Markers CDSB71 and pSB367 on MJ LG 22 and IND LG 21 were used to add IND LG 21 to HG 6. Markers CDSB53 and CSU428 on IND LG 21 and GG LG 20 were used to add GG LG 20 to HG 6. Markers pSB145 and CDSR17cI on IND LGs 10 and 47 and GG LG 20 linked the IND HG to add to the unified HG 6.

GG and IND shared three common markers on HG 6, while MJ and IND shared two common markers on HG 6.

Five (83%) of the six unique markers on MJ HG 6 correspond to sorghum LG F, while six (50%) of the 12 markers on IND HG 6 correspond to sorghum LG F.

A total of 13 probes detected 90 loci on HG 6. Thirty-three (38%) of them were mapped on 9 LGs forming HG 6. Among the 33 loci mapped, 30 (91%) correspond to sorghum LG F.

Sorghum LG G and *Saccharum* HGs 1 and 15

A total of five probes detected 45 loci on HG 15. Seventeen (38%) of them were mapped on 5 LGs forming HG 15. Among the 17 loci mapped, 14 (82%) correspond to sorghum LG G.

One HG in GG, previously designated HG 1, corresponds to a segment of sorghum LG G. GG HG 1 consists of four LGs: 5, 14, 36, and 37. Two HGs in IND, consisting of LGs 16 and 24, and 13 and 14, correspond to two segments of sorghum LG G. One HG in PIN, consisting of LGs 4 and 5, corresponds to a segment of sorghum LG G. On the basis of common markers, no original MJ HG corresponded to sorghum LG G.

Markers CDO202 and CDSB32 on GG LG 5 and PIN LG 40 were used to combine two HGs into a single HG 1. Using the unified HG 1 as a template, we found 10 additional LGs, including GG LGs 21, 22, 29, and 57, MJ LGs 7, 18, 19, and 50, and PIN LGs 11 and 21, could be added to HG 1. Markers CDSC19 and CDSB58 on MJ LG 18 and IND LGs 16 were used to add IND HG to the unified HG 1.

GG and MJ shared seven common markers on HG 1; GG and IND shared four markers, and GG and PIN shared six markers. MJ and IND shared four common markers; and MJ and PIN shared four markers. IND and PIN shared four common markers.

Among the 14 markers of GG HG 1, eight (55%) correspond to sorghum LG G. Six (55%) of the 11 unique markers on MJ HG 1 correspond to sorghum LG G, while one (7.7%) corresponds to sorghum LG C. Four (40%) of the 10 markers on IND HG 1 correspond to sorghum LG G, and two markers correspond to sorghum LG B. Seven (77%) of the nine markers on PIN HG 1 correspond to sorghum LG G. Two (40%) of the five markers on IND HG 15 correspond to sorghum LG G.

A total of 17 probes detected 171 loci on HG 1. Eighty-two (38%) of them were mapped on 19 LGs forming HG 1. Among the 82 loci mapped, 66 (80%) correspond to sorghum LG G.

Sorghum LG H and *Saccharum* HG 9

One HG in GG, consisting of LGs 44 and 45 and previously designated HG 9, corresponds to a segment of sorghum LG H. One HG in MJ, consisting of LGs 26, 27, 28, 33, and 40, corresponds to part of sorghum LG H. Two HGs in IND, consisting of LGs 8 and 23, and 30 and 33, correspond to two parts of sorghum LG H. One HG in PIN, consisting of LGs 7 and 19, correspond to part of sorghum LG H.

Markers pSB240 and pSB1248 on GG LG 45 and MJ LGs 28 and 33 were used to unite these two HGs to a single HG 9. Markers pSB240 and CDSC16 on MJ LGs 28 and 33, and IND LG 30 were used to add one of the two IND HGs to the unified HG9. Markers pSB1248 and CDSB57 on GG LGs 44 and 45, and IND LG 8 linked the other IND HG to HG 9. Markers CDSB57 and CDSB10 on IND LG 8 and PIN LG 19 linked PIN HG to HG 9. PIN LG 20 was added to HG 9 using the unified HG 9 as a template.

GG and MJ shared three common markers on HG 9; GG and IND shared three markers; and GG and PIN shared 2 markers. MJ and IND shared four markers; and MJ and PIN shared one marker; IND and PIN shared three markers.

Three (75%) of the four unique markers of GG HG 9 correspond to sorghum LG H. Six (66%) of the nine markers on MJ HG 9 correspond to sorghum LG H. Five (38%) of the 13 markers on IND HG 9 correspond to sorghum LG G, while two markers correspond to sorghum LG J and one to sorghum LG D. Two (50%) of the four markers on PIN HG 9 correspond to sorghum LG G.

A total of 11 probes detected 105 loci on HG 9. Fifty-nine (56%) of them were mapped on 13 LGs forming HG 9. Among the 59 loci mapped, 49 (83%) correspond to sorghum LG H.

Sorghum LG I and *Saccharum* HGs 7 and 17

One HG in GG, consisting of LGs 64 and 65 and previously designated HG 7, correspond to a segment of sorghum LG I. Two HGs in PIN, consisting of LGs 59 and 60, and 12 and 13, correspond to two parts of sorghum LG I. No LG in MJ and no HG in IND correspond to sorghum LG I.

Markers RG123 and pSB106 on GG LG 65 and PIN LG 60 were used to link these two HGs into a single HG 7. The other PIN HG, designed as HG 17, also corresponds to sorghum LG I. GG and PIN shared two common markers on HG 7.

Four (66%) of the six unique markers of GG HG 7 correspond to sorghum LG I. Both markers on IND HG 7 correspond to sorghum LG I. All three markers on IND HG 17 correspond to sorghum LG I.

A total of 4 probes detected 42 loci on HG 7. Sixteen (38%) of them were mapped to 4 LGs forming HG 7. Among the 16 loci mapped, 15 (94%) correspond to sorghum LG I.

A total of 4 probes detected 28 loci on HG 17. Eight (29%) of them were mapped to 2 LGs forming HG 17. All 13 loci mapped correspond to sorghum LG I.

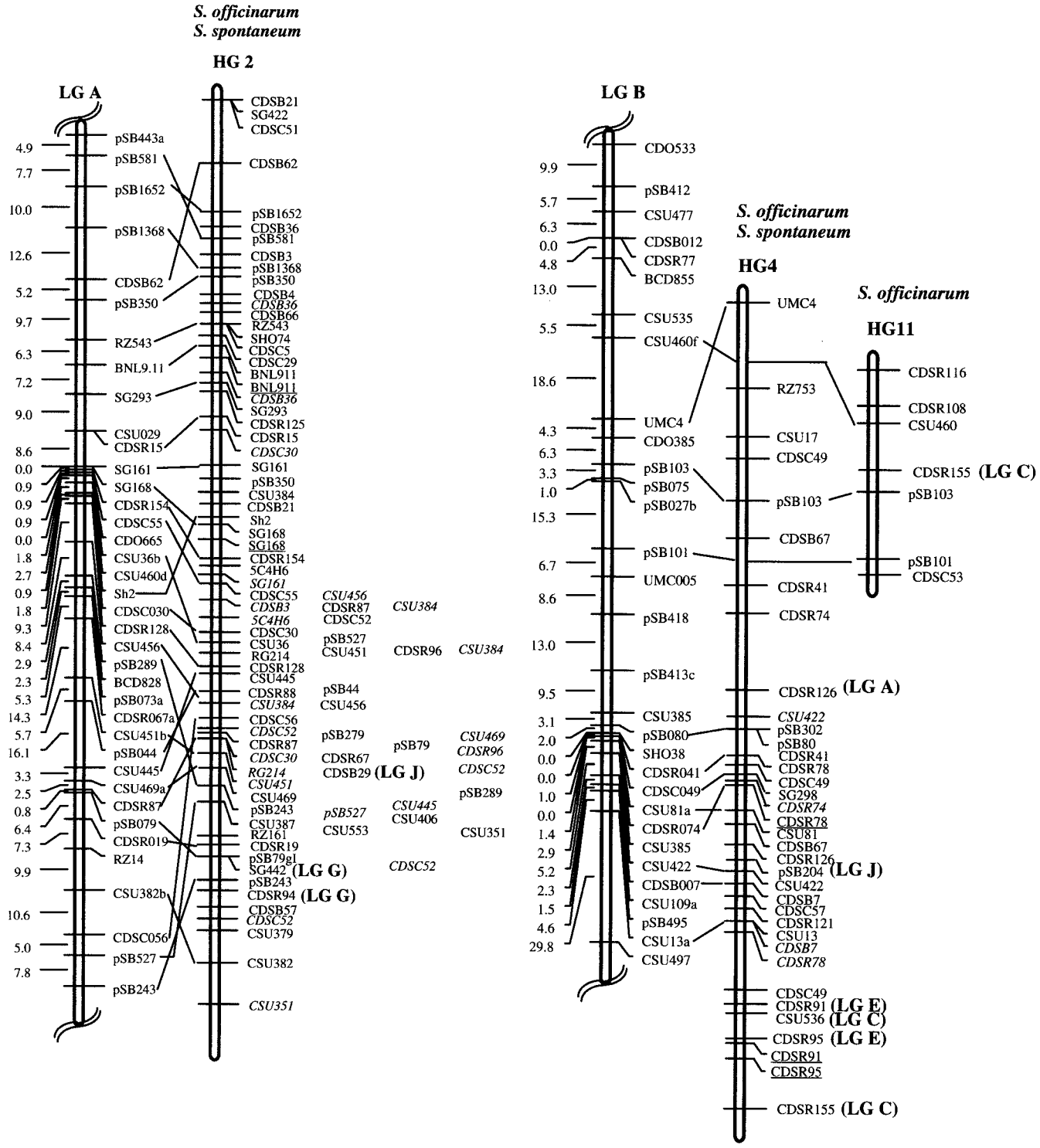

Fig. 1. Continued.

Sorghum LG J and *Saccharum* HG 10

One HG in GG, consisting of LGs 32 and 72 and previously designated HG 10, corresponds to a segment of sorghum LG J. One HG in IND, consisting of LGs 55 and 63, corresponds to part of sorghum LG J. One HG in PIN, consisting of LGs 48, 62, and 63, corresponds to part of sorghum LG J. No HG corresponds to sorghum LG I in GG or MJ.

Markers UMC47 and pSB149 on IND LG 55 and PIN LG 63 were used to link these two HGs into a single unified HG. Markers CDSR133 and pSB302 linked IND LG 31 to HG10. Markers UMC47 and pSB149 on IND LG 55 and GG LG 32 plus IND LG 31 linked all three HGs into HG 10.

GG and IND shared three common markers on HG 10; GG and PIN shared one marker. IND and PIN shared four common markers.

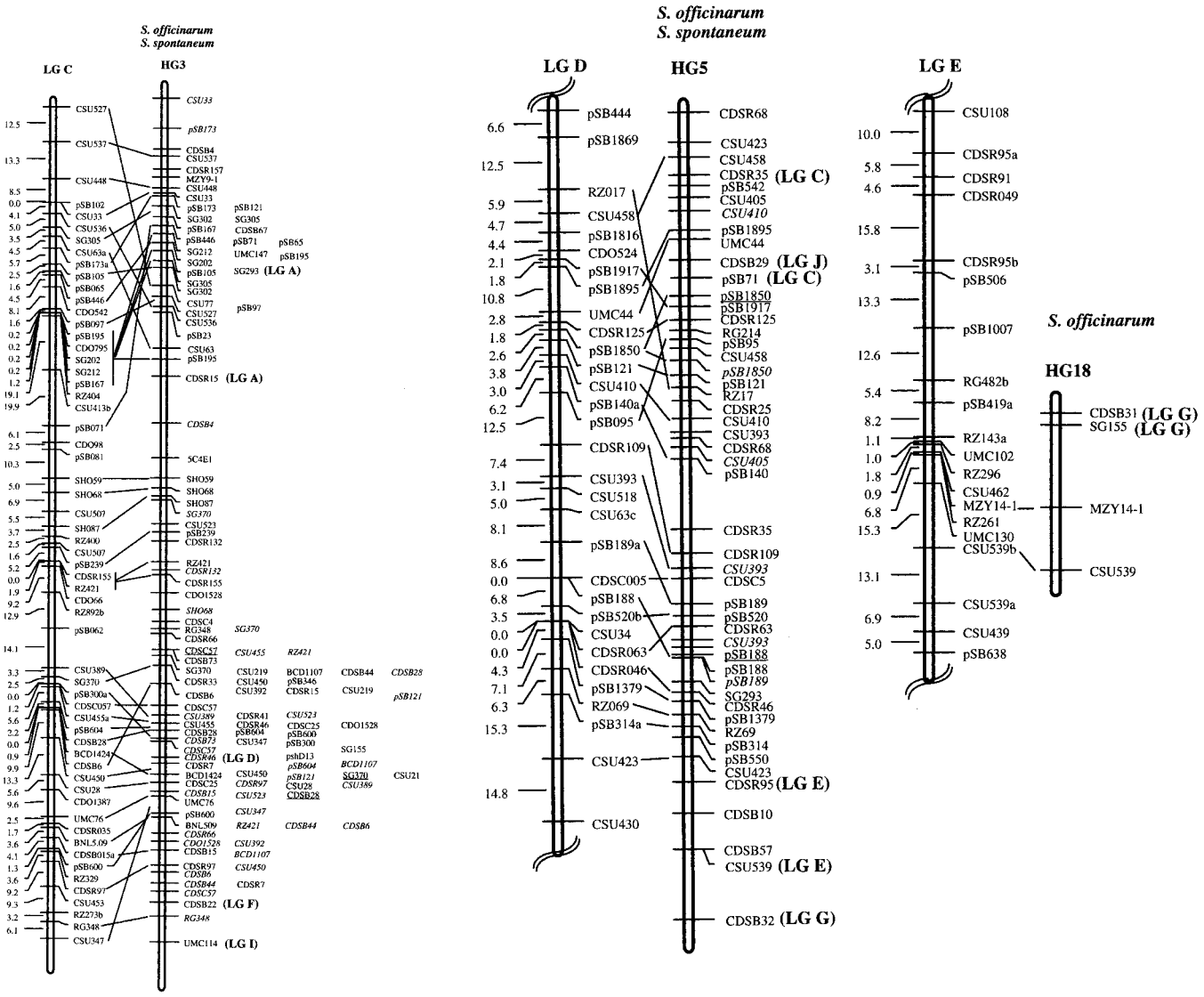

Fig. 1. Continued.

Three (57%) of the seven unique markers of GG HG 10 correspond to sorghum LG J. Five (71%) of the seven markers of IND HG 10 correspond to sorghum LG J. All six (100%) markers of PIN HG 10 correspond to sorghum LG J.

Only four (1.4%) of the 289 LGs in four sugarcane maps did not correspond to any of the sorghum LGs. These are GG LGs 19 and 74, and MJ LGs 30 and 36 (Fig. 1).

A total of 10 probes detected 80 loci on HG 10. Forty-one (51%) of them mapped to 9 LGs forming HG 10. Among the 41 loci mapped, 36 (88%) correspond to sorghum LG J.

Consensus Map

Using the sorghum linkage map as a template to condense the four sugarcane linkage maps permitted us to assemble 13 consensus HGs from 286 unique DNA markers (probes) (Table 4). Among the 183 (64%) of these 286 markers mapped in sorghum, 153 (84%) were mapped on the primary sorghum LG to which a particular sugarcane HG corresponded. Thirty (16%) were mapped to non-homologous sorghum LGs. Seventeen tandem duplication events and 56 other possible duplication events, based on relative position on different linkage groups, are seen on this sugarcane consensus map. Sixteen chromosomal rearrangements based on mapping information on one or more linkage groups might have occurred since the divergence of the sorghum and sugarcane genomes.

Sorghum LG A and Consensus HG 2

The consensus map of HG 2 was assembled from 38 LGs in GG, MJ, IND, and PIN (Fig. 1, Tables 5 and 6). Twenty-nine (52%) of the 56 markers on HG 2 correspond to sorghum LG A, while one (1.8%) corresponds to sorghum LG J, and two (3.6%) to sorghum LG G (Table 4). The marker order and relative position of eight markers, SG161 and CDSR154 on GG LGs 39 and 46, pSB279 and CDSB29 on GG LGs 10 and 11, pSB79 and pSB527 on MJ LGs 32 and 64, and Sh2 and

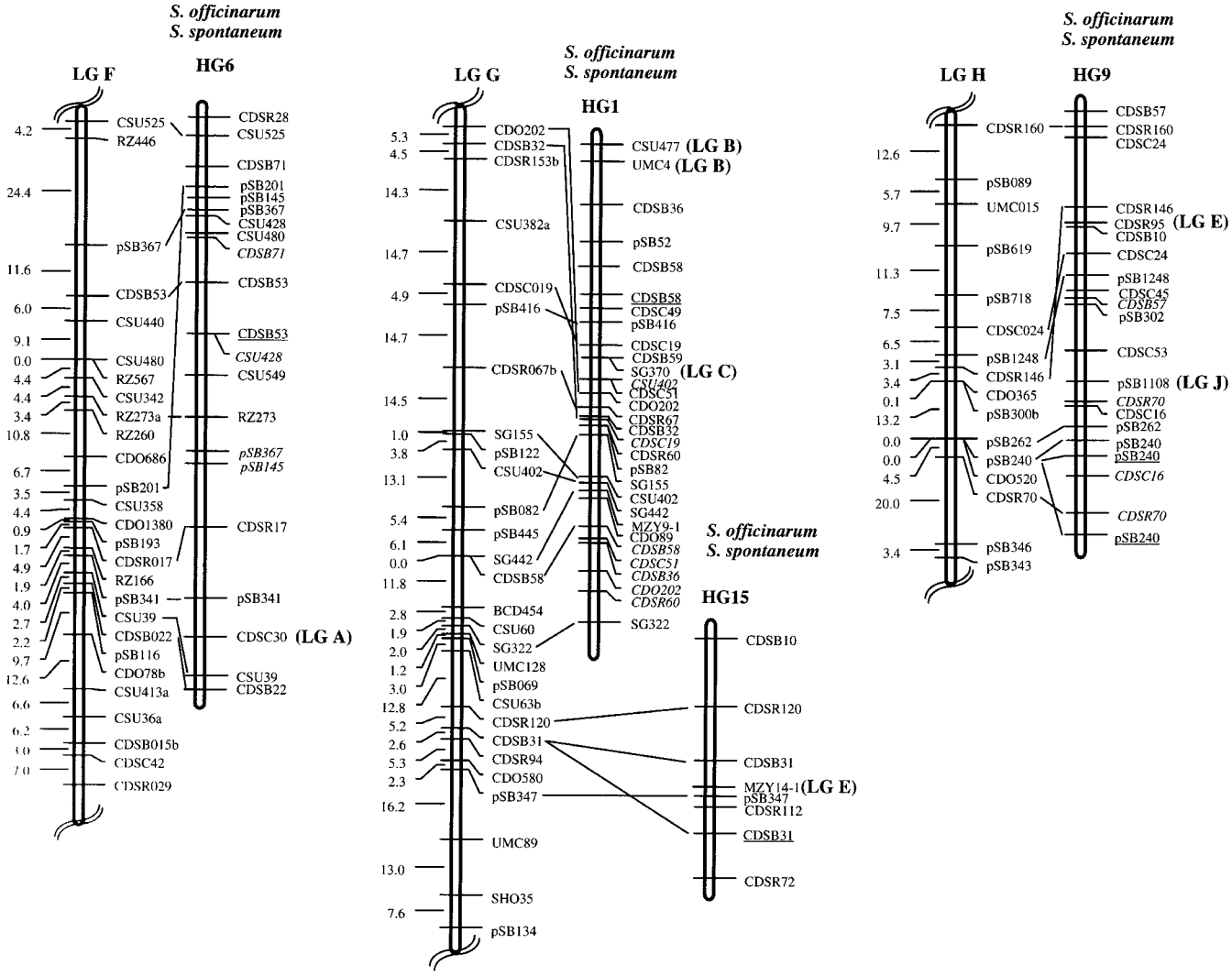

Fig. 1. Continued.

5C4H6 on PIN LGs 49, 71, and 72, were confirmed in two or more sugarcane LGs. SG168 on MJ LGs 63 and 66, and BNL9.11 on IND LG 4 are seen as tandemly duplicated markers. Another 11 repeated markers were identified on the basis of their relative positions to other linked markers.

A chromosomal rearrangement involving markers pSB581 and CDSB62 occurred on GG LGs 17 and 68 and IND LG 4. A second chromosomal rearrangement involved marker Sh2 and CDSC30 on GG LG 11, a third involved markers pSB350 on IND LG 5, and a fourth involved markers CSU469, pSB243, and pSB79 on IND LG 35.

Sorghum LG B and Consensus HG 4 and 11

The consensus map of HG 4 was assembled from 19 LGs in GG, MJ, IND, and PIN. Ten (37%) of the 27 markers on HG 4 correspond to sorghum LG B, while one (3.7%) corresponds to sorghum LGs A and J, and two each (7.4%) to sorghum LGs C and E. The marker order and relative position of six markers, CDSR78 and CSU13 on IND LGs 40 and 53, CDSC49 and CDSR74 on IND LGs 29 and 34, CSU422 and CDSR78 on PIN LGs 29 and 34, and CDSR78 and CDSR91 on PIN LGs 34 and 47, were confirmed in two or more sugarcane LGs. CDSR78 on GG LG28 and PIN LG47, CDSR91 on GG LG 28, and CDSR95 on MJ LG 53 are seen as tandemly duplicated markers. Another two repeated markers CDSB7 and CDSR74 were identified on the basis of their relative positions to other linked markers on PIN Lg28 and IND LG 29. A chromosomal rearrangement involving marker CSU422 occurred on GG LG 55.

The consensus map of HG 11 was assembled from GG LGs 41 and 47. Three (43%) of the seven markers on HG 11 correspond to sorghum LG B, while one (14%) corresponds to sorghum LG C. The marker order and relative position of pSB103 and pSB101 were confirmed on GG LGs 41 and 47. No tandem duplication or chromosomal rearrangement was observed on the short HG 11.

Sorghum LG C and Consensus HG 3

The consensus map of HG 3 was assembled from 32 LGs in GG, MJ, IND, and PIN. Forty (60%) of the 67 markers on HG 5 correspond to sorghum LG C, while

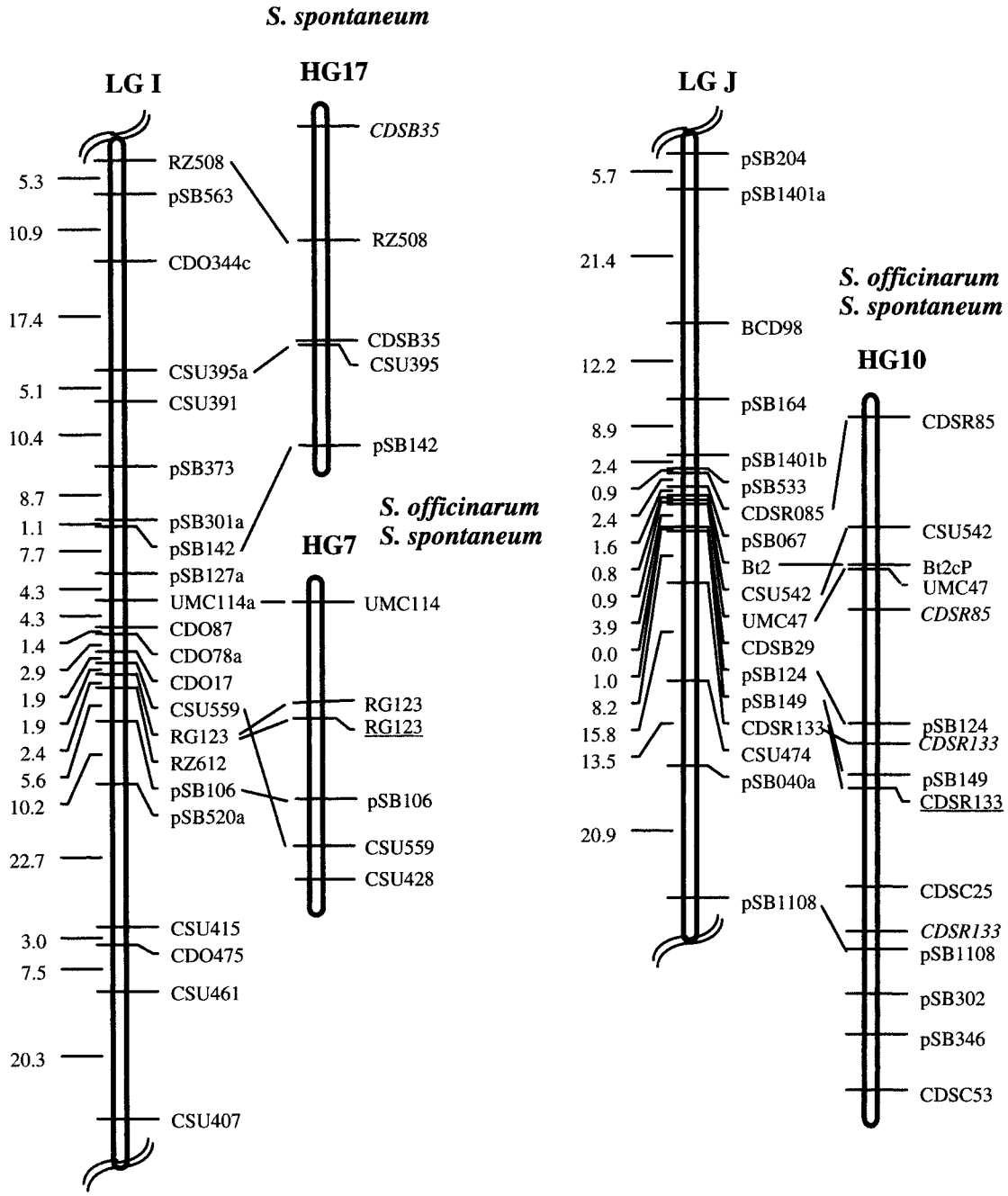

Fig. 1. ***Saccharum*** **consensus linkage map and corresponding sorghum linkage groups (LGs). Loci connected by a line are detected by the same probe in both genomes. The underlined markers were tandemly duplicated loci on a sugarcane linkage group. The italic markers, on the basis of their relative positions on different sugarcane linkage groups, might have been duplicated loci or might have been different alleles of the same loci on different homologs. This type of markers was referred as repeated loci to distinguish them from those tandemly duplicated loci on a single linkage group. Tandemly duplicated markers were connected by a line to the corresponding sorghum markers, but repeated markers were not connected. Markers on the right side of HGs 2 and 3 were approximately at the same location with the markers on the consensus map they aligned to. Markers mapped on a different sorghum LG were indicated by the sorghum LG in parentheses following the markers.**

one each (1.5%) corresponds to sorghum LGs D, F, and I, and two (3%) correspond to sorghum LG A. The marker order and relative position of 10 markers, pSB167, SG212, SG202, and SG302 on GG LGs 61 and 63, pSB173 and SG302 on GG LGs 48 and 60, CDSB6 and CDSB28 on MJ LGs 1 and 49, pSB600 and CSU523 on MJ LGs 6 and 25, CDSB6 and CDSC57 on IND LGs 27 and 28, and SHO59, SHO68, and SHO87 on IND LGs 43, 46, and 68, were confirmed in two or more sugarcane LGs. The duplicated markers were CDSC57 on GG LG1, SG370 on GG LG 3 and PIN LG 3, and marker CDSB28 MJ LGs 1 and 11 and IND LG 3. There were 28 repeated markers on consensus HG 3.

A chromosomal rearrangement involving markers pSB167, SG212, SG202, SG302, CSU536, and CSU527 occurred on GG LGs 61, 63, and 69. A second chromo-

Table 4. Homologous loci and chromosome rearrangements among *Saccharum* consensus HGs and *Sorghum* LGs.

Sorghum LG	*Saccharum* HG	Shared loci	Mismatched Loci	Tandem duplication	Repeated loci	Chromosomal rearrangement	Total loci
A	2	29	3	2	11	4	56
B	4	10	6	3	2	1	27
	11	3	1				7
C	3	40	5	3	28	5	67
D	5	22	6	2	3	2	43
E	18	2	2				4
F	6	9	1	1	3	1	15
G	1	11	3	1	5	1	22
	15	3	1	1			7
H	9	8	2	2	2	1	16
I	7	3		1			4
	17	4			1		5
J	10	9		1	1	1	13
Sum		153	30	17	56	16	286

somal rearrangement involved marker pSB71 on GG LG 49, a third involved markers CDSB6 and CSU28 on GG LGs 4 and 24, a fourth involved markers CDSR97, CDSB15, and UMC76 on GG LGs 2 and 9, and a fifth involved markers CDSB6 and CDSC57 on IND LGs 27 and 28.

Sorghum LG D and Consensus HG 5

The consensus map of HG 5 was assembled from 32 LGs in GG, MJ, IND, and PIN. Twenty-two (51%) of the 43 markers on HG 5 correspond to sorghum LG D. The marker order and relative position of 10 markers, RG214 and RZ17 on GG LGs 59 and 67, CDSR25 and pSB121 on MJ LGs 43 and 44, pSB188 and pSB189 on MJ LGs 59 and 61, UMC 44 and pSB95 on PIN LGs 39 and 40, and CSU458 and CSU405 on PIN LGs 53 and 54, and IND LG 52, were confirmed in two or more sugarcane LGs. The duplicated markers were pSB188 on MJ LGs 59 and 60, and marker pSB1850 on GG LG12. Another three repeated markers were SU405, CSU393, and pSB189 based on their relative positions on IND LG 41, GG LG12, and PIN LG 45.

A chromosomal rearrangement involving markers CSU410, pSB1850, UMC44, and CDSR125 occurred on IND LGs 41, 51, and 52. Another chromosomal rearrangement involved markers CDSR63, pSB188, and RZ69 on IND LG 49.

Sorghum LG E and Consensus HG 18

The short consensus map of HG 18 was assembled from two LGs in GG. Two (50%) of the four markers on HG 18 corresponds to sorghum LG E. The other two markers, CDSB31 and SG155, correspond to sorghum LG G, but were mapped on two separate LGs 18 and 15, respectively, undermining the possibility of chromosome fusion in regions corresponding to sor-

Table 5. Corresponding *Saccharum* linkage groups to homologous groups.

Saccharum HG	Linkage groups	
	GG	MJ
1	LGs 5, 14, 21, 22, 29, 36, 37, 53, 57	LGs 7, 18, 19, 50
2	LGs 10, 11, 15, 17, 38, 39, 46, 54, 68	LGs 4, 5, 10, 12, 13, 29, 32, 37, 42, 54, 63, 64
3	LGs 1, 2, 3, 4, 7, 8, 9, 24, 25, 26, 35, 43, 48, 49, 60, 61, 62, 63, 69, 70	LGs 1, 2, 3, 6, 11, 25, 40, 55, 58, 67, 68, 69, 70, 71
4	LGs 27, 28, 52, 55, 56	LGs 31, 41, 48, 53
5	LGs 6, 12, 40, 50, 58, 59, 66, 67	LGs 34, 43, 44, 45, 46, 51, 59, 60, 61
6	LG 20	LGs 22, 23
7	LGs 64, 65	
9	LGs 44, 45	LGs 26, 27, 28, 33
10	LGs 32, 72	
11	LGs 41, 47	
15	LG 13	LG 15
17		
18	LGs 73, 76	
Unassigned	LGs 19, 74	LGs 30, 36
	IND	PIN
1	LGs 16, 24	LGs 4, 5, 11, 21
2	LGs 4, 5, 17, 18, 32, 35, 36, 37, 38, 42	LGs 15, 28, 30, 35, 36, 46, 49, 50, 62, 71
3	LGs 1, 2, 3, 20, 22, 27, 28, 43, 46, 54, 68	LGs 1, 3, 16, 17, 44, 58, 64, 69
4	LGs 29, 34, 40, 48, 53	LGs 22, 25, 26, 29, 31, 33, 47
5	LGs 15, 41, 49, 51, 52, 60	LGs 6, 39, 40, 45, 51, 52, 53, 54, 65, 66
6	LGs 10, 11, 21, 47, 66, 60	
7		LGs 59, 60
9	LGs 8, 23, 30, 33	LGs 7, 19, 20
10	LGs 31, 55, 63	LGs 32, 48, 63
11		
15	LGs 13, 14	LG 8
17		LGs 12, 13
18		
Unassigned		

Table 6. Corresponding *Saccharum* homologous groups and unassigned linkage groups to *Sorghum* linkage groups.

Sorghum LG	Corresponding *Saccharum* homologous groups and unassigned linkage groups			
	GG	MJ	IND	PIN
A	HG 2	HG 2; LGs 35, 57, 66	HG 2; LG 56	HG 2; LGs 2, 38
B	HG 4; LGs 33, 42	HG 4; LGs 16, 24, 47, 52	HGs 4	HG 4; LGs 27, 70
C	HGs 3	HG 3; LGs 62, 72	HG 3; LGs 26, 39, 67	HG 3; LGs 18, 37, 43, 57
D	HG 5; LG 16	HGs 5; LG 14	HG 5; LGs 50, 65	HG 5; LGs 23, 28, 33
E	HG 4, 18; LGs 34, 75	HG 4; LGs 9, 56	LGs 9	LGs 9, 14
F	HG 6; LGs 23, 30, 31, 51	HG 6; LGs 8, 17, 20, 21	HG 6; LG 19	LGs 24, 41, 42, 68
G	HGs 1, 15	HGs 1, 15	HGs 1, 15; LG 25	HGs 1, 15; LG 10
H	HG 9; LG 71	HG 9; LGs 38, 40	HG 9; LG 45	HG 9; LG 67
I	HG 7; LG 18		LGs 6, 7, 57, 58, 59, 61, 64, 69	HGs 7; LG 55
J	HG 10	LGs 39, 65, 73	HG 10; LGs 12, 44, 62	HG 10; LGs 56, 61

ghum LGs E and G. The marker order and relative position of markers MZY14-1 and CSU539 were confirmed on GG LGs 73 and 76. No chromosomal rearrangement occurred on HG 18.

Sorghum LG F and Consensus HG 6

The consensus map of HG 10 was assembled from nine LGs in GG, MJ, and IND. Nine (60%) of the 15 unique markers on HG 10 correspond to sorghum LG J. The marker order and relative position of four markers, CDSB71 and pSB367 on MJ LGs 22 and 23, and pSB341 and CDSC30 on IND LGs 10, 11, and 70, were confirmed in two or more sugarcane LGs. The tandemly duplicated marker was CDSB53 on GG LG 20. The repeated markers were CDSB71, pSB145, and pSB367 based on their relative positions on IND LGs 21, 47, and 66. A chromosomal rearrangement involving marker pSB201 occurred on MJ LG 22.

Sorghum LG G and Consensus HG 1 and 15

The consensus map of HG 1 was assembled from 19 LGs in GG, MJ, IND, and PIN. Eleven (50%) of the 22 markers on HG 1 correspond to sorghum LG G, while one (4.8%) corresponds to sorghum LG C, and two (9.6%) correspond to sorghum LG B. The order and relative position of six markers, CDSB32 and SG155 on GG LGs 5, 22, and 37, CDSB58, CSU402 on IND LGs 16 and 24, and GG LG 5, CDO202, and CDSB32 on PIN LGs 4 and 5 and GG LG 5, were confirmed in two or more sugarcane LGs. CDSB58 on IND LGs 16 and 24, and GG LG 5 are duplicated markers. The repeated markers were CDSC19, CDSC51, CDSB36, CDO202, and CDSR60 based on its relative positions to other linked markers. A chromosomal rearrangement involving markers CDSC19, CDO202, and CDSB32 occurred on GG LGs 5, 22, 29, and 37, MJ LG 18, and IND LG 16.

The consensus map of HG 15 was assembled from GG LG 13, MJ LG 15, IND LGs 13 and 14, and PIN LG 8. Three (43%) of the seven markers on HG 15 correspond to sorghum LG G, while one (14%) corresponds to sorghum LG E. The order and relative position of markers CDSR120 and CDSB31 were confirmed on IND LGs 13 and 14. CDSB31 on GG LG 13 is a duplicated marker. No chromosomal rearrangement occurred on HG 15.

Sorghum LG H and Consensus HG 9

The consensus map of HG 9 was assembled from 13 LGs in GG, MJ, IND, and PIN. Eight of the 16 (50%) markers on HG 9 correspond to sorghum LG H, while one each (5%) corresponds to sorghum LGs E and J. The marker order and relative position of six markers, CDSR146, pSB1248, and pSB240 on GG LGs 44 and 45, pSB262 and pSB240 on MJ LGs 26 and 33, and pSB240 and CDSR70 on IND LGs 30 and 33, were confirmed in two or more sugarcane LGs. CDSC16 and pSB240 on IND LGs 28 and 33 are duplicated markers. CDSB57 and CDSR70 are considered as repeated markers based on their relative positions on GG LG 34, MJ LGs 27 and 28, and IND LGs 8, 23, 30, and 33. A chromosomal rearrangement event involving markers CDSR146, pSB1248, and pSB240 occurred on GG LGs 44 and 45.

Sorghum LG I and Consensus HG 7 and 17

The consensus map of HG 7 was assembled from four LGs, including GG LGs 64 and 65, and PIN LGs 59 and 60. Four (80%) of the five markers on HG 7 correspond to sorghum LG I. The marker order and relative position of markers RG123 and pSB106 were confirmed on PIN LGs 59 and 60. Tandem duplication of marker RG123 is seen on GG LG 64. No chromosomal rearrangement occurred on the current consensus map of HG 7.

The consensus map of HG 17 was assembled from PIN LGs 12 and 13. Three (75%) of the four markers on HG 17 correspond to sorghum LG I. Marker CDSB35 appeared to be duplicated. No chromosomal rearrangement occurred on the current consensus map of HG 17.

Sorghum LG J and Consensus HG 10

The consensus map of HG 10 was assembled from eight LGs, including GG LGs 32 and 72, IND LGs 31, 55, and 63, and three PIN LGs 48, 62, and 63. Nine (69%) of the 13 unique markers on HG 10 correspond to sorghum LG J. The marker order and relative position of four markers, CSU542 and UMC47 on IND LGs 55 and 63, and pSB124 and pSB149 on MJ LGs 48, 62, and 63, were confirmed in two or more sugarcane LGs. Marker CDSR133 was duplicated on GG LG 32. Marker CDSR85 might be also duplicated based on its relative position on IND LG 55 and PIN LG 48. A chromosomal

rearrangement involving markers CSU542, *Bt2* (maize probe of brittle endosperm2), UMC47, and CDSR85 occurred on IND LG 55 and PIN LG 48.

DISCUSSION

The overwhelming correspondence among the HGs of four *Saccharum* linkage maps to a particular *Sorghum* linkage group prompted us to assemble a *Saccharum* consensus map. We used a minimum of two common markers to connect corresponding HGs to form a single unified HG. Thirty-six of the 41 pair-wise comparisons shared more than half the markers on individual HGs ranging from three to 25 (Table 4). Among the 13 consensus sugarcane HGs, 11 HGs were shared by both *S. officinarum* and *S. spontaneum*, and only one short HG each was specific to either *S. officinarum* or *S. spontaneum*. Only 30 (10%) of the 286 loci on our *Saccharum* consensus map failed to match corresponding sorghum LGs. Sorghum is a close relative of sugarcane and it has been suggested that these two species may have diverged as little as 5 million years ago (Al-Janabi et al., 1994).

Despite fairly extensive genome mapping carried out on five different sugarcane populations, the sugarcane linkage map remains incomplete (Da Silva et al., 1995; Mudge et al., 1996; Grivet et al., 1996; Ming et al., 1998). Only about 70% of the sorghum genome is covered collectively by the four sugarcane maps GG, MJ, IND, and PIN (Ming et al., 1998) that we used to assemble the consensus map. The number of linkage groups exceeds the expected chromosome number (n) for each parent. This indicates that gaps remain on most if not all chromosomes. The large number of unlinked single dose markers, 145 (33%) for GG, 145 (40%) for MJ, 138 (35%) for IND, and 114 (37%) for PIN, reinforce the suggestion that these maps are incomplete. Theoretically the unlinked markers are at least 27.5 cM apart ($\theta = 0.25$, Ming et al., 1998), while the linked markers are much closer with an average of 8.5, 6.9, 8.5, and 7.2 cM for GG, MJ, IND, and PIN, respectively. Thus, the portion of unmapped homologs might be higher than the percentage of unlinked markers. On the other hand, when there are 6 (IND) to 14 (MJ) homologs per basic chromosome, the mapped linkage groups could represent a larger portion of the genome than indicated by the number of linked markers since only one or two homologs were mapped in part of the genome (http://www.plantgenome.agtec.uga.edu/sugarcane_maps.html; verified October 25, 2001). Our alignment of the *Saccharum* HGs with the *Sorghum* LGs provides a more accurate estimate of the sugarcane genome coverage by linkage groups.

The GG × IND cross appears to have higher recombination rates (average 8.5 cM for both GG and IND) than that of the PIN × MJ cross (6.9 and 7.2 cM for MJ and PIN, respectively). Further investigation is needed to determine whether the larger chromosome numbers (Table 1) were correlated negatively with recombination rates.

Although many chromosomal rearrangements appeared on the alignment of our *Saccharum* consensus map with the sorghum linkage map, only 16 of them were supported by at least one sugarcane linkage group. The remaining possible rearrangements were based on the relative positions of markers on different linkage groups, and may reflect differences in recombination rates rather than gene order.

The basic chromosome number of sugarcane has been determined by quantitative karyotyping and fluorescence in situ hybridization as $x = 10$ for *S. officinarum* and $x = 8$ for *S. spontaneum* (D'Hont et al., 1998; Ha et al., 1999). On the basis of the consensus map, HGs corresponding to sorghum LGs A, C, D, F, H, and J appear to be conserved in both *Saccharum* species. Part of the LG I is conserved in both species, but one part is only present in *S. spontaneum*. Chromosome fusion could have occurred in the genomic regions corresponding to sorghum LGs B and E in both *S. officinarum* and *S. spontaneum*, LGs B and G in *S. spontaneum* (IND), and LGs E and G in *S. officinarum* (GG) (Fig. 1 and also see http://www.plantgenome.agtec.uga.edu/sugarcane_maps.html). However, in *S. officinarum* separate HG 18 corresponds to part of LG E, and HG 11 corresponds to part of LG B. The 18S–25S rDNA was located at the terminal position of a set of chromosomes in *S. officinarum*, but at an interstitial position of chromosomes in *S. spontaneum* (D'Hont et al., 1998). This might indicate structural differences involving chromosome fusion between these two species. Evidence from our consensus map suggests that chromosome fusion could have occurred in genomic regions corresponding to sorghum LGs B and E, or B and G in *S. spontaneum*. Although HG 4 in *S. officinarum* corresponded to sorghum LGs B and E as well, the chromosome numbers of current GG ($2n = 97$-117) and MJ ($2n = 140$) (Burner, 1997) suggested that these two so-called *S. officinarum* accessions could be *Saccharum* spp. hybrids. The chromosome numbers of original Green German and Muntok Java were determined by Bremer (1923) and Rao and Vijayalakshmi (1962) as $2n = 80$. The two clones represented as Green German and Muntok Java, used in the mapping project, may very well be hybrids of unknown ancestry. Some sugarcane cultivars have 10% of the genome derived from *S. spontaneum* (D'Hont et al., 1996). If the other parent was *S. spontaneum*, the HG 4 could be *S. spontaneum* specific, especially considering HG 11 and HG 18 in *S. officinarum* correspond to LG B and E, respectively (Fig. 1). Two markers on LG 34 in PIN corresponded to HG 11, and this could be a segment of a rearranged *S. spontaneum* HG sharing homologous regions with HG 11.

HGs 3 and 8 were combined by means of a few common markers, but the links were not convincing. The gap might correspond to the centromere of the homologous maize chromosome (Paterson et al., 1995). A more saturated map is needed to confirm whether these two HGs are truly joined. Seven of 10 basic chromosomes of *S. officinarum* appear likely to correspond to sorghum LGs A, D, F, G, H, I, and J. The other three chromosomes may correspond to LGs B, C, and E, with or without inter-chromosomal rearrangements. Six of the eight ba-

sic chromosomes of *S. spontaneum* appear to correspond to sorghum LGs A, D, F, H, I, and J. The other two chromosomes could correspond to LGs B, C, E, and G with inter-chromosomal rearrangements involving chromosome fusion or fission. Complete sugarcane consensus maps will be needed before drawing firm conclusions about the occurrence of inter-chromosomal rearrangements after the divergence of *Saccharum* and *Sorghum*.

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